TEMPERATURE AND LIGHT AS FACTORS INFLUENCING THE RATE OF SWIMMING OF LARVÆ OF THE MUSSEL CRAB, PINNOTHERES MACULATUS SAY

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Significant and numerous studies have been made in the past on the phototropism of plants and animals, and the quantitative aspects of the effect of light on photosensory systems have been extensively studied by Hecht and others; however, little is known concerning photokinesis and the effect of temperature on free-moving, light-sensitive organisms. Some investigators have even denied an effect of light on the behavior of such forms other than on orientation. Davenport and Cannon (1897) found an apparent difference in rate of swimming of *Daphnia* in full light as compared with swimming under one-fourth this intensity, but they concluded that this was probably due not to a change in velocity but to more rapid and accurate orientation at the higher intensity. Yerkes (1900) substantiated the findings of Davenport and Cannon on *Daphnia* and found in addition a slight effect of intensity on rate of swimming of *Cypris,* but he came to similar conclusions, namely, that the apparent change in rate was due primarily to changes in accuracy and rapidity of orientation. In neither of these investigations was a very wide range of intensities used. Their conclusions agree with those of the majority of observers before and since, with few exceptions. Moore and Cole (1921) found that the rate of locomotion of *Popillia japonica* during upward geotropic progression was influenced by light and that the rate of movement was a function of the light intensity. Cole (1922*a*) obtained similar results regarding the upward creeping of *Drosophila,* and (1922*b*) found a distinct effect of light on the rate of creeping of *Limulus.* Mast (1923) expresses doubt regarding the validity of Moore and Cole's (1921) results on *Popillia* for he states that they did not exclude the time required for the insects to orient and get under way. Mast also doubts the value of Loeb's (1890) observations on rate of movement of aphids as a function of light intensity, for he claims that temperature was not eliminated as a factor. Mast and Gover (1922) studied the effect of intensity of light and rate of locomotion of *Phacus* and *Euglena,* and although with

Euglena they found what may be a significant increase in rate at high intensities, they nevertheless concluded that light intensities sufficient to cause rapid and accurate orientation need not have any additional appreciable effect on rate.

The lack of agreement regarding the photokinetic effect of light, and the fact that the problem has considerable bearing on our proper understanding of movements of plankton organisms, led to an attempt to gain additional information. Crustacean larvae form one of the representative groups of the animal plankton of the sea and were found to be most satisfactory for the work as planned. The work was carried out during the summer of 1931 at the Woods Hole Oceanographic Institution. It was made possible largely through the kindness of Dr. H. B. Bigelow, Director of the Institution, and the author wishes to acknowledge his appreciation for the excellent facilities and equipment placed at his disposal. The author is also indebted to Professor W. J. Crozier for suggestions in the preparation of the paper.

Material and Methods

For the study of photokinesis a suitable animal should possess certain characteristics which have been lacking in part in many of the animals previously studied. They should be positive or negative to light; they should orient accurately and rapidly; they should move in a straight line; they should preferably be aquatic organisms, in order to make it possible easily to control the temperature. In addition to these requirements any satisfactory experimental animal must be obtainable in large numbers over a considerable period of time, or must be easily reared or kept in the laboratory.

For satisfying these requirements it is difficult to conceive of a more suitable form than the young larvæ of *Pinnotheres maculatus* Say, the mussel crab. The adults are found living as parasites in the mantle cavity of *Mytilus edulis,* the edible mussel. Sixty-five per cent of the mussels collected from a bed near Grassy Island, Woods Hole, were infested with these crabs so the adults were easily obtained. A considerable number of females carrying eggs were found at all times during July and August. These are easily kept in the laboratory in bowls of sea water, and one can have one or more batches of larvæ hatching daily, each batch containing several hundred individuals.

The larvæ are distinctly positive to light. They orient with head away from the light and by means of forward strokes of the swimming appendages move backward toward the light. This is similar to the orientation of the young larvæ of the lobster as observed by Hadley

(1908), and of the young larvæ of *Palaemonetes* as described by Lyon (1906). At all light intensities used there was extremely rapid orientation consuming only a fraction of a second, and the larvæ took a course toward the light which was a straight line in most cases.

At a given light intensity and temperature the velocity of movement was quite constant for individuals of a given age, but after two or three days the rate of swimming decreased and at the age of four to five days the larvæ had a tendency to be temporarily negative; this necessitated using larvæ of known age.

As a careful control of either temperature or light intensity is necessary when studying the effect of the other factor, all experiments were performed in a dark room; by means of a water-bath, the temperature could be accurately controlled, and with proper methods light of the desired intensity obtained.

The water-bath consisted of a 30-gallon insulated tank with 4 x 6 inch plate glass windows set in opposite sides and near one end. Temperatures below room temperature were obtained by means of a cooling unit similar to one described by Stier (1931), with a mercury thermoregulator operating a heating unit of 100-watt capacity. Rate as a function of light intensity was studied for the most part at temperatures slightly above room temperature which obviated the necessity of using the cooling device. The water in the tank was stirred by means of a motor-driven agitator, and was changed at frequent intervals in order to avoid loss of light by suspended particles which tended to accumulate in the tank.

The light-source was a 6-volt, 18-ampere, ribbon filament lamp, shielded by means of a double housing in order to prevent leakage of light. The light passed through lenses which kept the rays practically parallel. The intensity was controlled by means of Wratten neutral tint filters, which, used singly or in combination, transmitted the following percentages of the original light: 50, 25, 10, 5, 2.5, 1, 0.5, 0.1, 0.05 per cent. The beam of light passed through a series of screens with apertures of the proper size, and through ground glass for diffusion. A second light for attracting the larvæ to the opposite end of the trough consisted of a Spencer lamp with a 150-watt bulb and ground glass.

The larvæ were placed in filtered sea water in a trough of plate glass with inside dimensions 29 x 4 x 4 cm. This trough was covered with a glass plate and submerged to within a half centimeter of the top in the water of the bath. Here it was supported on hangers so that it was always at a given distance from the light source and so that the beam of light just covered the inside section of the trough and, the rays being parallel, reflection of light from the glass sides was negligible.

Measurements of the light intensity within the trough were made by means of a Macbeth Illuminometer, by putting a small test plate in the water of the trough. The intensity of light at the end of the trough nearest the ribbon filament lamp (the variable source) when no filters were used was found to be 93 meter candles. The 150-watt lamp at the distance used gave an intensity of 68 meter candles at the end nearest this lamp.

By means of the neutral filters it was possible, without changing the distance of the lamp from the tank, to obtain the following intensities of light at the end of the trough nearest the ribbon filament lamp: 46.5, 23.3, 9.3, 4.7, 2.3, 0.93, 0.47, 0.093, and 0.047 meter candles. The last intensity was the lowest that it was practical to use, for below this it was impossible to see the larvæ distinctly and even at this intensity it was necessary for the observer to be adapted to complete darkness before making each observation. There was, of course, considerable absorption of light by the sea water of the trough, and the intensity at the far end in each instance was considerably lower than the intensity given for the near end, and this varied throughout the trough; however, the total light reaching the larvæ as they swam from the far end to the near end of the trough was proportional to the intensity at the near end, and varied as this was varied.

In preliminary experiments observations were made on the rate of swimming of individual larvæ as compared with the rates of the first or middle member of a small swarm, and the variations were no greater in the second instance than in the first. As it was more often possible to complete a series of data if several individuals were used instead of one, a small swarm of 10–25 animals was used in most of the experiments. The writer realizes the possibility of greater variations in the results when swarms are studied but in this particular instance the behavior of several larvæ selected from a given batch showed as great uniformity as did single individuals, at least when the fastest and slowest members had been discarded.

In a particular experiment a group of larvæ were selected of the proper age and placed in the trough and adapted to the temperature of the water-bath for at least a half hour. They were then attracted by the 150-watt light to the end of the trough away from the variable light source, and their swimming movements would keep them in close contact with the glass in their endeavors to continue their course toward this light. This light would then be cut off and at the same time the light at the opposite end turned on and a stop watch started. The time necessary for the fastest individual or group of individuals to traverse the 29 cm. was then taken. At a given light intensity or temperature

either five or ten trials were made and the results averaged.   In this way
it was possible to determine the rate of swimming of the larvæ both
as a function of temperature and light intensity.   As stated above the
extremely rapid orientation of the larvæ and the apparent absence of a
latent period obviated the necessity of considering these factors and
made the measurements easier and more accurate than would have been
true with many free-swimming forms.

TEMPERATURE AND VELOCITY OF LARVÆ AT A CONSTANT LIGHT INTENSITY

Preliminary observations indicated a decided effect of temperature
on the rate of swimming of the larvæ, and although only one series of
measurements on individuals of the same age was made over a wide

TABLE I

Effect of temperature on rate of swimming of larvæ at a constant light intensity

Temperature	Time for swimming 29 cm. (Averages of 10 readings)	P.E. of time	Velocity $\frac{1}{\text{time for 29 cm.}}$
° C.	seconds		
27.0	12.38	± 0.100	0.0806
25.9	13.09	± 0.090	0.0763
24.8	14.53	± 0.046	0.0690
23.5	15.50	± 0.057	0.0645
22.0	17.70	± 0.099	0.0565
20.0	20.70	± 0.127	0.0483
18.5	24.79	± 0.175	0.0403
17.6	25.64	± 0.117	0.0391
16.5	27.72	± 0.139	0.0361
15.2	32.30	± 0.152	0.0310
14.2	36.11	± 0.149	0.0277
13.4	39.05	± 0.302	0.0256

range of temperatures, the results from this were quite significant.
The range of temperatures used was from 27.0° C. to 13.4° C.   The
light toward which the larvæ swam was kept at a constant intensity of
93 meter candles.   The results are shown in Table I.   The times given
for swimming 29 cm. are, at each temperature, averages for ten read-
ings.   Between different temperatures one hour was allowed for adapta-
tion to the new temperature.

From these results one can determine the time for swimming a meter
at different temperatures.   At 27.0° this was 43.4 seconds, under the
conditions of the experiment; at 18.5° the same larvæ required 1 minute
27 seconds for travelling a meter; and at 13.4°, 2 minutes 16.5 seconds.

Temperature changes in the sea are slow and comparatively small yet this factor must be of some importance in determining the rate of movement of plankton organisms, particularly when near the surface.

The probable errors of the times are shown in Table I and it may be seen that these are not large. There is a rather definite relationship between the average time for swimming 29 cm. and its probable error, and it is interesting to note that they are both affected by temperature in much the same way; as the mean time increases, the P.E. increases in proportion. The significance of this has been pointed out by Crozier (1929) and Navez (1930).

A plot of velocity against temperature centigrade (Fig. 1) indicates that the increase in velocity with increasing temperature is not on a simple smooth curve; it is evident that one curve does not fit the results. There is a break near 18.5° and near this point occurs the one velocity measurement which does not conform fairly well with the rest. It will
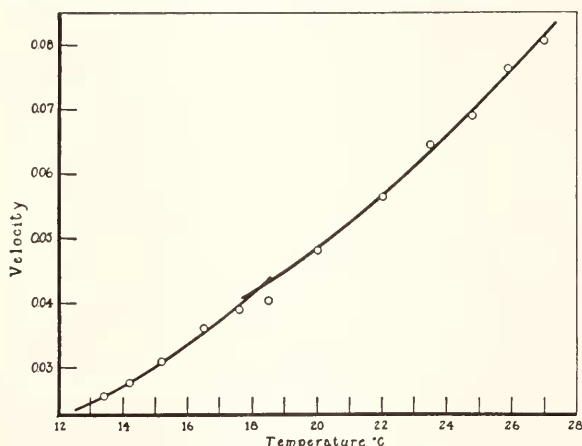

Fig. 1. Data of Table I plotted as velocity (reciprocal of time for 29 cm.) against temperature centigrade. Two curves are shown which intersect between 18° and 19°. This break is more evident when the same data is plotted as in Fig. 2.

be seen in Table I that the mean time from which this velocity was obtained has a high P.E. compared with those above and below. When the logarithm of the velocity is plotted against the reciprocal of the absolute temperature (Fig. 2) it is more apparent that between 13.4° and 27.0° two lines must be drawn to fit the data; these lines are straight and intersect at about 18.5°, thus indicating that the Arrhenius equation $\left[\dfrac{K_2}{K_1} = \epsilon^{\frac{\mu}{2}\left(\frac{1}{T} - \frac{1}{T_2}\right)}\right.$ where K_1 is the velocity at $T_1°$ Abs., and K_2 the velocity at $T_2°$ Abs.; $\epsilon = 2.718$; μ is a constant over a certain tempera-

ture range and designated by Crozier as a " temperature characteristic "]
holds for the rate of swimming of these larvæ as a function of tempera-
ture. The values of μ as calculated are 16,900 below 18.5° and 12,800
above 18.5°. It is not necessary to go into the significance of these
values and of the break, or critical temperature, for this has been done
by Crozier (1924) and others, for many cases which are fundamentally
similar; it is sufficient to note that corresponding values for μ have been
frequently encountered in studies of the influence of temperature on
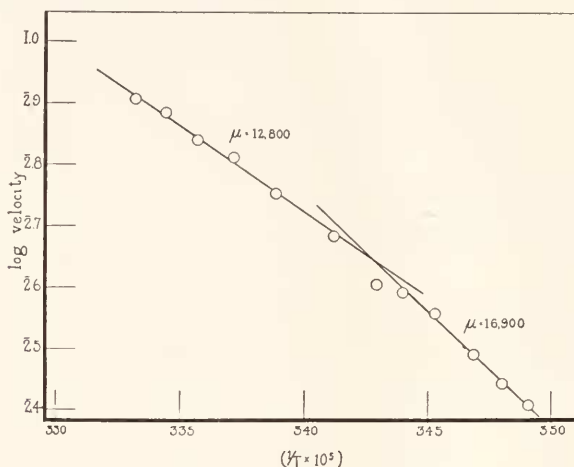rate of many biological processes.

Fig. 2. Same data as in Fig. 1, plotted as the logarithm of velocity against
the reciprocal of absolute temperature $\times 10^5$. That two lines must be drawn to fit
the data is evident.

Few studies of the effect of temperature on the rate of locomotion of
organisms have been made, the only other on a free-swimming form with
which the writer is familiar is that of Glaser (1924) for *Paramecium*.
He found that the Arrhenius equation could be applied, and secured a
value for μ of 16,000 below 16° and of 8,000 above 16°.

It is realized that changes in density and viscosity of the sea water
occur with changes in temperature and these factors enter in, and intro-
duce slight errors in the measurements which are difficult to eliminate.
To what extent they are significant remains to be seen.

The effect of temperature on the velocity of swimming at different
light intensities will be discussed in a later section.

LIGHT INTENSITY AND THE RATE OF SWIMMING OF LARVÆ AT A CONSTANT TEMPERATURE

The importance of temperature as a factor influencing the rate of
swimming of *Pinnotheres* larvæ has been indicated in the previous sec-

tion.   During the work on the photokinetic effect of light the temperature was carefully controlled and kept constant, for a given series, within ± 0.1°.

In addition to temperature, age was found to be an important factor ·influencing the rate of locomotion, and although this was not carefully investigated the age was taken into consideration in the later determinations of the effect of intensity of light.   Because either age or temperature varied between separate series of experiments in some of the earlier work, it was impossible to average or compare much of the data, although the results were fundamentally similar.   As an example of the effect of age on rate of movement it is necessary to cite only one instance. On August 23 at 2:00 P.M. a certain larva swam the 29 cm. in 14.2 seconds, in a light intensity of 93 meter candles; on August 24 at 10:00 A.M. the same individual required 15.2 seconds to swim the same distance.   In each case the times as given are averages for five readings. It was also found that over a range of intensities, larvæ 30 hours old were less sensitive to the light than larvæ 15 hours old.   It is obvious that age would not be of such importance if one were dealing with adult animals, but in the case of crustacean larvæ, as is well known, a few days makes a great difference in the responses of the animals to light (Hadley, 1908, and others).

Early in the course of the work on light intensity it was found that changes in rate of swimming were obtained over a comparatively small range of intensities.   The maximum velocity, at temperatures near 23°, was reached at approximately 25 meter candles.   This suggests that in much of the previous work on the photokinetic effect of light, intensities above the minimum necessary for eliciting a maximum response may have been used, and the conclusions that light intensity has no effect on rate of locomotion are perhaps unjustified in many instances.   It is logical to assume that aquatic organisms are sensitive to a lower range of intensities of light than are land organisms, for they live constantly at reduced intensities.

It should also be pointed out that the intensity of light to which the animals are previously adapted affects to a certain extent the rate of movement in subsequent intensities.   Several trials were made to determine the effect of dark adaptation on rate of movement in the light, with the expectation that for a few trials the animals would swim more rapidly, due perhaps to an accumulation of a photosensitive material in the light receptors.   In every instance the first few trips, after dark adaptation of several hours, occupied more time than subsequent trips.   This phenomenon is perhaps similar to that noted by Davenport and Cannon (1897), who found that *Daphnia* responded more quickly and accurately

to the light after having made several trips in it.   Hecht (1925) also
found in *Ciona* that after dark adaptation of several hours the first re-
action time to a given intensity of illumination was definitely longer
than those which followed, and which remained constant for long pe-
riods.   These authors offered no explanation and as yet there seems
to be no satisfactory reason why this should be true.   The following
experiment seems somewhat contradictory in view of these results on
dark adaptation.   Larvæ were adapted to a series of light intensities
ranging from 0.093 to 93.0 meter candles and the time for swimming
toward a light of 68 meter candles subsequently obtained.   The results
are shown in Table II.   After adaptation to light of 0.093 meter candles
13.4 seconds were consumed in swimming 29 cm., in an illumination of
68 meter candles.   This time increased as the intensity of the adapting

TABLE II

Effect of intensity of adapting light on time for swimming 29 cm. toward light of constant intensity.   Age of larvæ 30 hours.   Temperature 25.4° C.

Intensity of adapting light	Intensity of attracting light	Time for swimming 29 cm. toward light of 68 meter candles
meter candles	*meter candles*	*seconds*
0.093	68	13.4
0.93	68	13.3
4.7	68	13.9
9.3	68	14.2
23.3	68	14.2
46.5	68	14.3
93.0	68	14.7

light increased, until after adaptation to 93.0 meter candles 14.7 seconds
were required for swimming the same distance.   This indicates a dis-
tinct effect of the adapting illumination, and in the experiments to follow
the larvæ were, in every case, adapted to light of a constant intensity
before each trial. ·

From several series of experiments to determine the velocity of
swimming in intensities ranging from 0.093 or 0.47 meter candles to
93.0 meter candles very uniform results were obtained.   The maximum
rate of swimming was reached in light of about 25 meter candles, and
although this rate varied somewhat the variation was due to differences
in age of the larvæ, temperature of the water, or in some instances per-
haps to slight differences between given lots of larvæ or individual larvæ.

Table III gives one such series of data on larvæ 20 hours old, at a temperature of 24.5°. In this series readings were begun at the higher intensities and the intensities of the variable light source decreased by definite amounts between sets of readings. Progression from low to high intensities yields essentially the same results. In this particular series the faster individuals in the swarm travelled the 29 cm. in 16.6 seconds, at an intensity of 93.0 meter candles. At 46.5 meter candles there was no significant change. At 23.3 meter candles the time for swimming 29 cm. had increased to 17.5 seconds and from this intensity down to 0.47 meter candles, the lowest intensity tried, there was a gradual increase in time ; at the lowest intensity the time being almost exactly twice as great as at the higher intensities.

A plot of this data as reciprocal of the time against the light intensity

TABLE III

Effect of light intensity on rate of swimming of larvæ at a constant temperature (24.5° ± 0.1). Series 8.6. Age of larvæ 20 hours.

Intensity	Time for 29 cm. (Averages of 5 readings)	P.E. of time	Velocity $\dfrac{1}{\text{time for 29 cm.}}$
meter candles	*seconds*		
0.47	33.9	± 0.91	0.0295
0.93	31.8	± 0.80	0.0315
2.3	27.2	± 0.70	0.0368
4.7	23.5	± 0.57	0.0426
9.3	21.5	± 0.62	0.0465
23.3	17.5	± 0.31	0.0571
46.5	16.7	± 0.41	0.0599
93.0	16.6	± 0.22	0.0602

yields a smooth curve as seen in Fig. 3. One point does not fall well on the curve but, as may be seen in Table III, the probable error of the time at this intensity (9.3 meter candles) is high in comparison with those above and below. The velocity at 93.0 meter candles is not shown on the graph as it is practically the same as that at 46.5 meter candles. It should be noted that in no instance were rates of swimming obtained in very low intensities or in total absence of light, for obvious reasons. It should also be pointed out that swimming movements of crustacean larvæ do not stop even in absence of light ; instead the larvæ remain at or near the surface, kept there by constant but random movements.

One might expect, if the effect of light on rate of locomotion could be determined in the same way as the effect on orientation of the larvæ,

to find them obeying the Bunsen-Roscoe Law as did Loeb and Northrop (1917) in their investigation of the orientation of *Balanus* larvæ to a two-point source of light. If this law held for velocity of locomotion, the relationship between velocity and light intensity would be a linear one. That this is not true is quite evident, and the reason is perhaps obvious. Loeb and Northrop were concerned with the degree of turning of the path toward the stronger of two lights and this in no way depended on previous velocity and to only a very slight extent on water resistance.

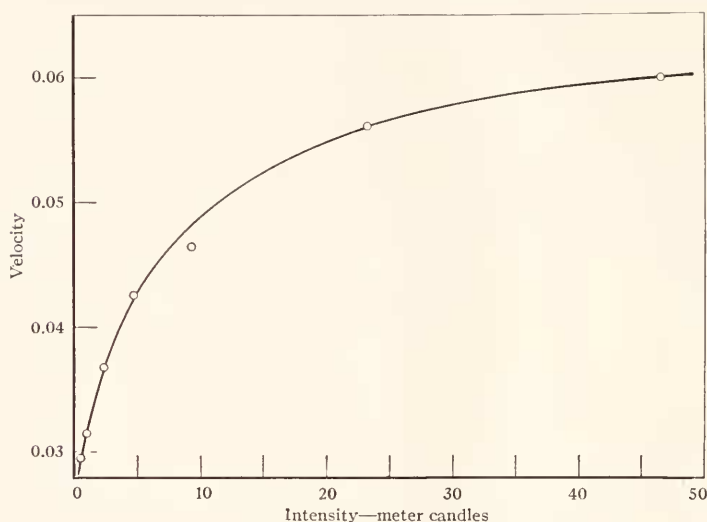The results obtained (Fig. 3) more nearly resemble those obtained

Fig. 3. Data of Table III, Series 8.6, plotted as velocity against intensity (meter candles). See text.

by Moore and Cole (1921) for rate of movement of *Popillia japonica* as related to light intensity, and later by Cole (1922) for *Drosophila*. In both of these instances they found apparent conformity with the Weber-Fechner Rule, as Henri (1912) had claimed for the reactions of *Cyclops* to ultra-violet light, and Patten (1915) when using a graded series of absolute intensities of opposed lights in studying orientation of blowfly larvæ. Although such conclusions are to a certain extent unwarranted by the fact that the Weber-Fechner Rule does not hold for intensity discrimination in certain forms, as pointed out by Hecht (1924, 1928), yet the approximate linear relation of response plotted against the logarithm of intensity is sometimes useful in analyzing such data. Crozier (1928) in discussing the case of *Limax,* where the

amount of turning per unit length of path is directly proportional to the logarithm of the light intensity, emphasizes the fallacy of considering this an obeyance to Weber's Rule and yet suggests that the same empirical treatment is useful, where other perhaps more significant treatments are impractical.

If the data given in Table III are plotted as velocity against the logarithm of the intensity, the relationship is found to be far from linear. This indicates that the velocity is not related directly to the logarithm of the intensity of illumination. In the work of Moore and Cole on the Japanese beetle they were dealing with an organism which, under a ruby light or in the dark, seldom showed any movement, but which was aroused to activity by illumination from any direction. As has been pointed out above, *Pinnotheres* larvæ are constantly moving even in total absence of light, and this initial velocity must bear some relation to later velocities produced by illumination.
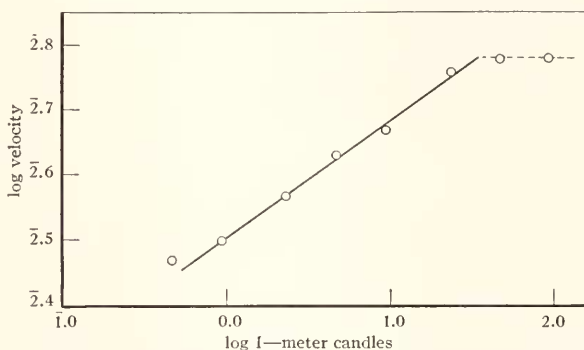

Fig. 4. Complete data of Series 8.6 plotted as logarithm of velocity against logarithm of intensity. The graph is essentially rectilinear until the maximum velocity of swimming is approached.

If we assume that the velocity of movement (V) is so related to the light intensity (I) that any increase in velocity (ΔV), produced by a small increase in intensity (ΔI), is a function of the velocity and also inversely proportional to the intensity, we obtain the following expression:

$$\frac{\Delta V}{\Delta I} \propto \frac{V}{I}.$$

Upon integration this yields the following equation:

$$\log V = k \log I - C$$

where k is the constant for the slope of the line, at any given temperature, and C is an integration constant. This expression indicates the way in

which the slope of the curve of velocity plotted against intensity depends, at any point, on both the previous velocity and light intensity. It may be checked by altering another variable such as temperature as is shown in the following section. If we apply this formulation to the data in Table III and plot the logarithm of velocity against the logarithm of intensity, we obtain a straight line over most of the range of intensities as shown in Fig. 4. Two velocities are shown at intensities of 46.5 and 93.0 meter candles which were obtained at or near the maximum velocity possible at this temperature, and which, of course, do not fall on the curve as drawn, but between 0.47 and 23.3 meter candles the straight line fit is good.

The theoretical significance of such an empirical treatment need not concern us. It is sufficient that we have a convenient method for com-

TABLE IV

Effect of light intensity on rate of swimming of larvæ at different temperatures. Age of larvæ 15 hours.

INTENSITY	SERIES 8.21 A TEMP. 13.4 ° ± 0.1 °		SERIES 8.21 B TEMP. 18.0 ° ± 0.1 °		SERIES 8.21 C TEMP. 27.1 ° ± 0.1 °	
	Time for 29 cm.	P.E. of time	Time for 29 cm.	P.E. of time	Time for 29 cm.	P.E. of time
meter candles	*seconds*		*seconds*		*seconds*	
0.093					22.8	± 0.28
0.47			39.2	± 0.62	18.3	± 0.28
0.93	86.7	± 2.16	35.9	± 1.04	17.1	± 0.06
2.3	64.7	± 1.06	31.0	± 0.39	15.2	± 0.21
4.7	56.8	± 0.89	27.0	± 0.35	13.7	± 0.09
9.3	47.7	± 0.53	23.9	± 0.32	13.5	± 0.11
23.3	39.7	± 0.30	22.4	± 0.33	13.3	± 0.17

paring data obtained by varying the several factors such as temperature, light intensity, and age, which so evidently influence the rate of swimming.

THE EFFECT OF LIGHT INTENSITY ON RATE OF SWIMMING OF LARVÆ AT DIFFERENT TEMPERATURES

In the preceding sections we have shown the effect of temperature on the velocity of *Pinnotheres* larvæ at a constant light intensity, and the effect of light intensity at a constant temperature. Now it might be of value to compare light intensity curves from larvæ of the same age obtained at different temperatures.

Table IV gives three series of data on larvæ 15 hours old, at tem-

peratures of 13.4°, 18.0° and 27.1° C. The complete range of light intensities available was not used at each temperature, for the rate of swimming was extremely slow and rather irregular below an intensity of 0.93 meter candles, at the lowest of the three temperatures; however, sufficient determinations were made for adequate comparisons.

The curves for velocity plotted against light intensity are shown in Fig. 5. It may be seen that with increasing temperature, there is distinct displacement of the curves upward, and an earlier arrival at the maximum rate of swimming as the temperature increases. Also the slope of the curves changes with the temperature. At the lowest temperature the curve is much flatter than at the higher temperatures. While it was impossible to determine the effect of temperature upon
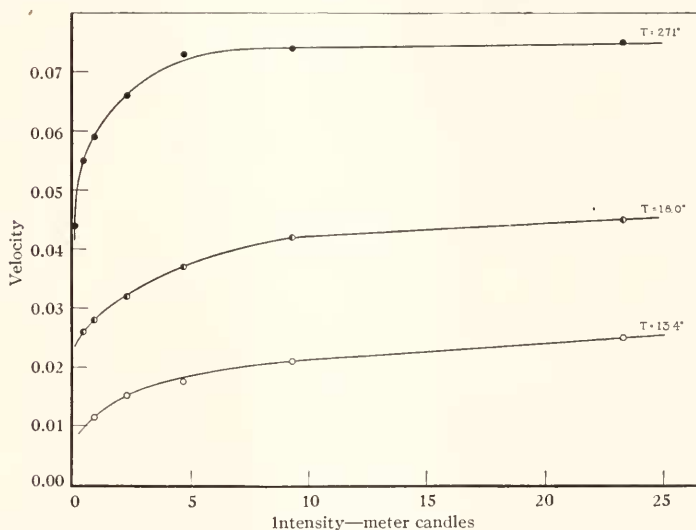

Fig. 5. Plot of data of Table IV as velocity against intensity. Open circles are Series 8.21 *A*; half-closed circles, Series 8.21 *B*; closed circles, Series 8.21 *C*. Temperatures as indicated.

the velocity of swimming in absence of light, it will be seen that there is a distinct effect on rate of locomotion in the dark, and if the curves were begun at the zero point on the abscissa, they would intercept the ordinate at varying levels above zero, depending upon the temperature. This is due to changes in rate of general activity, and to changes in the viscosity of the sea water. While no attempt has been made to correct for viscosity changes due to changes in temperature, these are of considerable importance. It was shown by Ostwald (1903, *a* and *b*) that in comparison with water, which might be considered to have a viscosity

of 100 at 0° C., sea water of 30 per cent salinity has a viscosity of 102, and this is reduced to 52 at 25° C. Thus sea water at 25° C. is approximately half as viscous as that at 0° C., and the same body would sink twice as fast at 25° C. as at 0° C. Viscosity changes with changes in temperature would therefore account for an appreciable part of the change in speed of swimming.

If we plot the data of Table IV as the logarithm of the velocity against the logarithm of the light intensity, we obtain as before essentially rectilinear graphs (Fig. 6), which vary in slope and in position relative to the abscissa. As in Series 8.6 (Fig. 4), the points representing velocities at or near the maximum do not fall on the lines, but over a definite range of intensities the straight line fit is good. The relative displacement of the graphs, and therefore the value of C in the
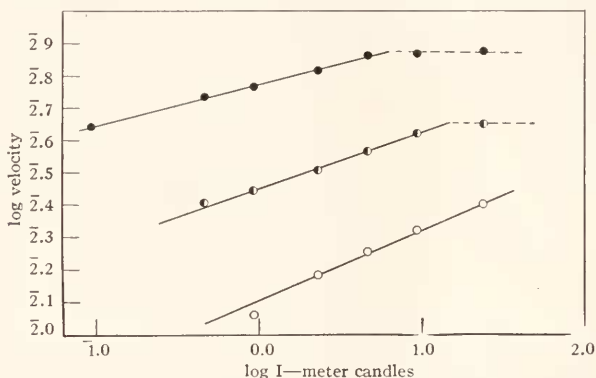

FIG. 6. Data of Table IV plotted as logarithm of velocity against logarithm of intensity. Symbols representing Series as in Fig. 5. See text.

expression $\log V = k \log I - C$, is seen to change considerably with a change in temperature. In addition, the slope of the lines is also seen to change. At 13.4°, k has a relative value of 0.225; at 18.0° $k = 0.175$; at 27.1° $k = 0.125$. At a given temperature the effect of increasing the intensity of illumination, within certain limits, is to increase the velocity. The changes in slope of the lines in Fig. 6 indicate the effect of temperature on the relation between velocity and intensity. At 27.1° the slope is less than at the lower temperatures, and the maximum rate of swimming is attained at a lower light intensity than at 18.0°. The expression

$$\frac{\Delta V}{\Delta I} \propto \frac{V}{I}$$

implies that if V be increased by operation of a variable independent of

I, the effect of increasing I must be correspondingly less—which is the fact. We have seen that temperature and light play an important part in determining the rate of locomotion of a crustacean larva. Other factors such as age and changes in viscosity of the surrounding medium must also be taken into consideration.

Summary

1. Larvæ of *Pinnotheres maculatus* Say are shown to be satisfactory animals for the study of photokinesis. The velocity of swimming is found to be greatly influenced by temperature and light intensity. Age, although not carefully investigated at present, is also an important contributing factor in determining the rate of locomotion.

2. A series of measurements of the effect of temperature on the velocity of swimming, at a constant light intensity, showed the applicability of the Arrhenius equation, and yielded values of μ of 12,800 above 18.5° and 16,900 below 18.5° C.

3. The larvæ are found to be sensitive to only a small range of light intensities. At temperatures between 20–25° C., the maximum possible velocity of swimming is attained at intensities between 10 to 25 meter candles. When velocity is plotted against light intensity a smooth curve is obtained. The same data when treated empirically according to the equation $\log V = k \log I - C$, yields essentially rectilinear graphs which are more satisfactory for a comparison of such data.

4. When series of measurements are made to determine the effect of light at different constant temperatures it is found that, besides a marked effect on general activity, there is a change in the relationship of velocity to intensity; the slopes of the curves change, and the maximum possible velocity of swimming for each temperature is reached earlier at the higher temperatures.

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